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Trans-generational effects on ageing in a wild bird population

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senescence.

Abstract

Ageing, long thought to be too infrequent to study effectively in natural populations, has recently been shown to be ubiquitous, even in the wild. A major challenge now is to explain variation in the rates of ageing within populations. Here, using 49 years of data from a population of great tits (*Parus major*), we show that offspring life-history trajectories vary with maternal age. Offspring hatched from older mothers perform better early in life, but suffer from an earlier onset, and stronger rate, of reproductive senescence later in life. Offspring reproductive lifespan is, however, unaffected by maternal age, and the different life-history trajectories result in a similar fitness payoff, measured as lifetime reproductive success. This study therefore identifies maternal age as a new factor underlying variation in rates of ageing, and, given the delayed trans-generational nature of this effect, poses the question as to proximate mechanisms linking age-effects across generations.

Introduction

Senescence, a late-life reduction in reproductive performance and/or survival probability, is thought to have evolved because unavoidable extrinsic mortality weakens the force of natural selection with age (Fisher, 1930; Medawar, 1952; Williams, 1957; Hamilton, 1966). This so-called 'selective shadow' led to a long-held belief that senescence would seldom be observable in natural populations (Hayflick, 2000; Kirkwood & Austad, 2000), yet longitudinal studies of various vertebrate populations have recently provided compelling evidence for its ubiquity (Jones *et al.*, 2008; Nussey *et al.*, 2008). Age-specific deterioration has been found both for survival (Loison *et al.*, 1999; Descamps *et al.*, 2008; Jones *et al.*, 2008; Keller *et al.*, 2008) and for various reproductive traits, including measures close to fitness, such as the number of offspring that survive to breed (Brommer *et al.*, 2007; Wilson *et al.*, 2007; Descamps *et al.*, 2008; Bouwhuis *et al.*, 2009).

Whereas declines in average performance with age within individuals are now well established, relatively little is known about whether rates of deterioration vary between individuals and, if so, which factors and mechanisms underlie these differences. First lines of evidence suggest that accelerated senescence may be associated with conditions early in life, specifically harsh environmental conditions [in red deer *Cervus elaphus* (Nussey *et al.*, 2007) and common guillemots *Uria aalge* (Reed *et al.*, 2008)] or high levels of reproductive effort [in red deer (Nussey *et al.*, 2006) and red squirrels *Tamiasciurus hudsonicus* (Descamps *et al.*, 2008)]. As yet unconsidered for natural populations, but the focus of an extensive body of work on laboratory model systems, is the possibility of maternal age at conception having long-term effects on offspring life histories (Mousseau & Fox, 1998a). These laboratory studies have not addressed the rates of ageing as such, yet some have focused on offspring lifespan, and found that offspring born from older mothers suffer from a reduced lifespan (Priest *et al.*, 2002; Tarin *et al.*, 2005). This pattern is referred to as the Lansing effect, after early work on rotifers *Rotifer vulgaris* by Albert Lansing (Lansing, 1947). Fitness consequences of a Lansing effect will depend on whether the reduction in offspring lifespan includes a reduction in reproductive

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lifespan, an issue which has received surprisingly little attention.

We examined trans-generational maternal age-effects by testing for a relationship between maternal age and offspring age-specific reproduction and reproductive lifespan. We used a large data set spanning 49 years of monitored breeding in a passerine bird, the great tit *Parus major*, for which we have previously shown reproduction to be age-specific, and senescence to occur (Bouwhuis *et al.*, 2009). Our analyses reveal maternal age to be associated with offspring age-specific reproduction, but not reproductive lifespan, and as such identify a new factor underlying variation in rates of ageing in wild populations.

Material and methods

Study population and data collection

The great tit is a small passerine bird, which has been studied at the c. 380 ha mixed deciduous woodland of Wytham Woods, Oxfordshire, UK, since 1947. From 1960 to 2008, 1020 nest boxes have been available for breeding, of which on average 217 were used by great tits each year. Nest boxes are checked every breeding season to obtain records of laying date, clutch size (i.e. number of eggs laid), brood size (i.e. number of chicks hatched, calculated as the difference between clutch size and the number of eggs left in the nest) and number of fledglings. Chicks are ringed with individually numbered metal rings 15 days post-hatching. Breeding birds are trapped at the nest whilst feeding their chicks, and identified by their ring number, or ringed if they are newly immigrated birds. Parental age is based on year of birth for locally hatched birds, or plumage characteristics (Svensson, 1994) at first catching for immigrants. Although immigration rates are high (47%, McCleery *et al.*, 2004), most immigrants enter the population as yearlings, such that exact age is known for 91% of birds. Birds first caught with adult plumage are assigned a minimal age of 2. Birds that are not found breeding for two consecutive years are assumed to have died, and their age at last reproduction (ALR) is taken as an estimate of their reproductive lifespan (also see Bouwhuis *et al.*, 2009).

Data selection

Previous analyses of age-specific reproduction in our population (Bouwhuis *et al.*, 2009) focused on first broods by females of known reproductive lifespan only, because (1) Wytham great tits very rarely produce a second brood (McCleery & Perrins, 1989), (2) data on male reproductive performance are less complete and confounded by extrapair paternity and (3) reproductive lifespan (i.e. ALR) is an important factor to include in models aiming to estimate within-individual patterns of a dependent variable with age (van de Pol & Verhulst,

2006). In addition, breeding attempts which were subject to experimental manipulation were included for assessment of ALR, but excluded from analyses of reproductive performance, whilst assuming no carry-over effects to the next breeding season (Doligez *et al.*, 2002). Here, we used the same data selection criteria, but for analyses of offspring age-specific reproduction, we furthermore selected only breeding attempts by females hatched from known-aged mothers. This resulted in a data set of 3722 breeding attempts by 2482 female offspring hatched from 1725 known-aged mothers.

Statistical analyses

Offspring age-specific reproduction

Models testing for the effect of maternal age on offspring age-specific reproductive performance were based on the minimal adequate models reported in (Bouwhuis *et al.*, 2009). In short, these four models had clutch size, brood size, number of fledglings or number of recruits as dependent variables, and included fixed effects of female age, female age², female ALR, year quality estimated as the total average fledgling number and local breeding density. The effect of maternal age was tested by also including maternal age, maternal age*female age, maternal age*female age² and maternal ALR as fixed effects. Random effects included female identity, year and sector of the wood to account for repeated, nonindependent observations on the same bird and spatiotemporal environmental heterogeneity, respectively. Models were additive cross-classified random effect models fitted in MLwiN 2.02 using a Markov chain Monte Carlo estimation algorithm and 100 000 iterations (Rasbash *et al.*, 2005; Browne *et al.*, 2007). The error structure used was normal for clutch size, brood size and number of fledglings, and Poisson for number of recruits. The full model (Table 1) was simplified by backward stepwise removal of nonsignificant terms, where significance was assessed using the Wald statistic. Note that if statistical tools allowing additive cross-classified random effect models for parameters with a combination of normal and Poisson error structures were available in a multivariate framework, the analyses described earlier could be combined in a single, multivariate analysis testing for overall effects of female and maternal age, or for age-effects on each reproductive trait whilst taking into account the covariance between these traits. At present such a modelling framework is, to the best of our knowledge, not available; hence, we report analyses of each dependent variable separately.

Offspring reproductive lifespan and lifetime reproductive success

To test the effect of maternal age on offspring reproductive lifespan (measured as ALR), and lifetime reproductive success (LRS, defined as the total number of recruits produced), we used two random effect models with

Table 1 Additive cross-classified random effect models testing the effects of female age, maternal age and selected fixed effects on clutch size, brood size, number of fledglings and number of recruits.

	Clutch size			Brood size			No. of fledglings			No. of recruits		
	Est	SE	Chi	Est	SE	Chi	Est	SE	Chi	Est	SE	Chi
Year quality	0.51	0.07	60.49*	0.56	0.08	47.85*	0.97	0.05	405.18*	0.35	0.05	40.77*
Local density	−0.34	0.06	30.90*	−0.44	0.07	37.25*	−0.43	0.10	18.60*	−0.18	0.07	6.45**
Age	0.55	0.14	14.44*	0.32	0.17	3.72	0.24	0.32	0.56	−0.05	0.13	0.16
ALR	0.02	0.03	0.46	0.02	0.03	0.40	0.09	0.05	3.27	0.03	0.02	2.25
Mat_age	0.03	0.08	0.12	−0.18	0.09	3.88**	−0.16	0.16	1.02	−0.08	0.07	1.20
Mat_ALR	−0.05	0.03	3.11	−0.03	0.03	0.72	0.02	0.04	0.16	0.03	0.02	2.04
Age ²	−0.07	0.03	6.26**	−0.04	0.03	1.57	−0.01	0.06	0.05	0.03	0.02	1.16
Mat_age*age	0.02	0.07	0.09	0.23	0.08	7.76***	0.20	0.15	1.79	0.11	0.07	2.91
Mat_age*age ²	−0.01	0.01	0.13	−0.05	0.02	8.21***	−0.04	0.03	2.32	−0.03	0.01	4.23**
Female (r)	1.14	0.07		0.96	0.08		1.39	0.21		0.09	0.05	
Year (r)	0.13	0.04		0.22	0.07		0.01	0.01		0.13	0.04	
Area (r)	1.25	0.05		2.16	0.08		5.83	0.22		0.01	0.01	

Estimates for random effects are marked by (r). Shown are parameter estimates with standard errors and significance (* $P < 0.001$, ** $P < 0.05$, *** $P < 0.01$).

ALR, age at last reproduction.

Poisson distributed errors and a Markov chain Monte Carlo estimation algorithm and 100 000 iterations in MLwiN 2.02. The models included maternal identity as a random effect to account for the fact that some offspring were hatched from the same mother. Fixed effects included in models for both female ALR and LRS were maternal age, maternal age², maternal ALR and the interactions between maternal ALR and age.

Grand-recruits

Using all females for which we knew the number of grand-recruits produced by their daughters, i.e. 8023 breeding attempts by 5310 individual females, a first model testing the effect of female age on number of grand-recruits included fixed effects of female age, female age², female ALR, female status (locally born vs. immigrant, 2-level class variable), year quality and local breeding density, and random effects of female identity, year and sector of the wood. In the second model, number of recruits was added as an extra covariate, to test whether age-effects surpassed those shown to affect their own offsprings' recruitment (Bouwhuis *et al.*, 2009). As described earlier, models were additive cross-classified random effect models fitted in MLwiN 2.02 using a Markov chain Monte Carlo estimation algorithm and 100 000 iterations.

Results

Offspring age-specific reproduction

Our previous analyses of age-specific reproduction revealed significant female age² effects on four successive reproductive traits: clutch size, brood size, number of fledglings and number of recruits (Bouwhuis *et al.*, 2009). For 3722 breeding attempts by 2482 female

offspring, aged 1 to 8, hatched from 1725 mothers of known age, we tested whether this quadratic effect of age interacted with the female's mother's age when she was hatched (maternal age, range 1–7 years) to explain reproductive performance. For clutch size, we found no evidence for such an interaction (Table 1), showing that females hatched from different-aged mothers show the same change in clutch size with age (Fig. 1a). For brood size, however, the interaction between maternal age and offspring age² was significant (Table 1), such that offspring hatched from older mothers display a more pronounced decline at old age in the number of chicks they hatch than offspring hatched from younger mothers (Fig. 1b). For the number of young fledged, the parameter estimate for the interaction was identical to that for brood size, but failed to reach statistical significance (Table 1, Fig. 1c). For the number of recruited offspring, the interaction between maternal age and offspring age² was again statistically significant (Table 1), the fitted model indicating higher early life reproductive output for offspring hatched from older mothers, but an earlier onset and stronger rate of senescence afterwards (Fig. 1d, and also see the Table S1 for analyses of the effect of maternal age per offspring age class).

Offspring reproductive lifespan and lifetime reproductive success

Among female recruits, ALR averaged 1.85 and ranged from 1 to 8 years. There was no evidence for a quadratic ($\text{mat_age}^2 = -0.006 \pm 0.009$, $\chi^2_1 = 0.425$, $P = 0.514$) or linear ($\text{mat_age} = -0.013 \pm 0.019$, $\chi^2_1 = 0.519$, $P = 0.471$) effect of maternal age at hatching on offspring ALR (Fig. 2). There was, however, a nonsignificant tendency for maternal reproductive lifespan (which ranged from 1 to 9 years) to covary positively with

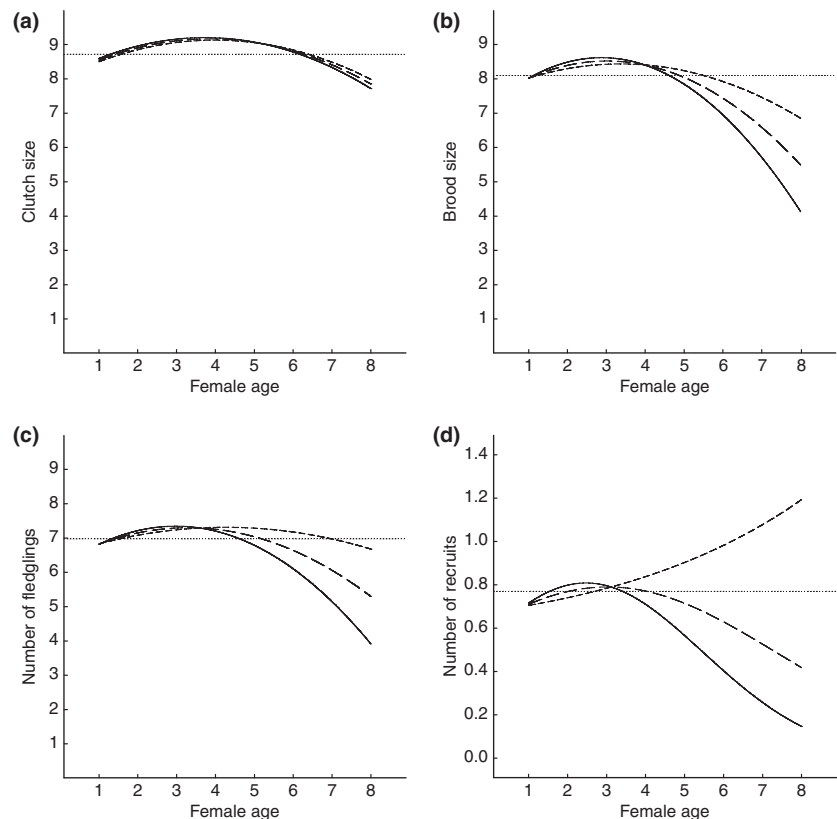


Fig. 1 Age-specific reproductive performance in female great tits in relation to the age of their mother when they were hatched: (a) clutch size, (b) brood size, (c) number of fledglings, and (d) number of recruited offspring. Lines are the fitted values representing females hatched from mothers one standard deviation younger than average (short dash), females hatched from average-aged mothers (long dash) and females hatched from one standard deviation older than average-aged mothers (solid); the dotted line shows the overall mean.

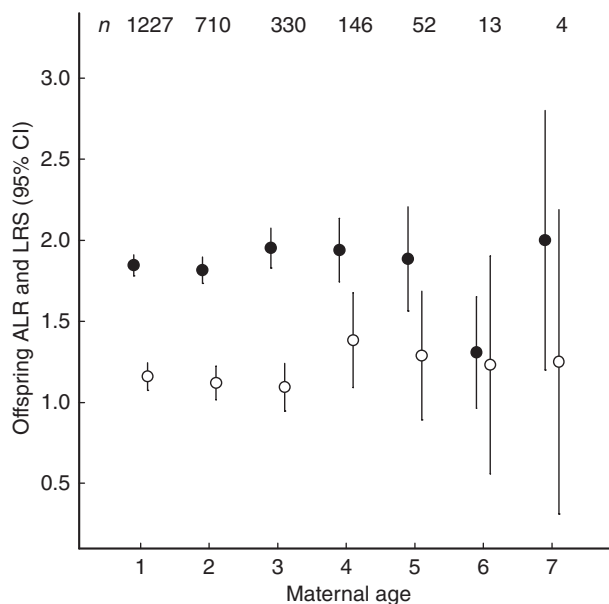


Fig. 2 Reproductive lifespan (age at last reproduction (ALR), black circles) and lifetime reproductive success (LRS, white circles) in female great tits in relation to the age of their mother when they were hatched, with 95% confidence intervals and sample size.

offspring reproductive lifespan ($\text{mat_ALR} = 0.017 \pm 0.010$, $\chi^2_1 = 3.032$, $P = 0.082$).

Female offspring LRS averaged 1.26 and ranged from 0 to 14 recruits. Again, there was no significant effect of maternal age, either quadratic ($\text{mat_age}^2 = 0.000 \pm 0.015$, $\chi^2_1 = 0.001$, $P = 0.975$), or linear ($\text{mat_age} = -0.032 \pm 0.029$, $\chi^2_1 = 1.230$, $P = 0.267$, Fig. 2). There also was no effect of maternal reproductive lifespan ($\text{mat_ALR} = 0.029 \pm 0.019$, $\chi^2_1 = 2.292$, $P = 0.130$) on offspring LRS.

Grand-recruits

As offspring LRS does not vary with maternal age, a female's number of grand-recruits should mainly depend on her number of recruits, instead of her age. Indeed, our analyses of a female's number of grand-recruits shows that her age is an important predictor when her number of recruits is not included as a covariate in the model, but is no longer significant when the number of recruits is added (Table 2).

Discussion

Recently, several long-term studies have demonstrated age-specificity in recruit production (Brommer *et al.*, 2007; Wilson *et al.*, 2007; Descamps *et al.*, 2008;

Table 2 Additive cross-classified random effect models testing the effects of female age and selected fixed effects on her number of grand-recruits without (left) and with (right) the number of recruits as a covariate.

	No. of grand-recruits			No. of grand-recruits		
	Est	SE	Chi	Est	SE	Chi
No. of recruits	N/A			1.11	0.03	1514.99***
Year quality	0.43	0.10	20.16***	0.13	0.09	2.03
Local density	-0.37	0.14	7.26**	-0.17	0.12	2.10
Status	0.15	0.08	3.29	0.05	0.08	0.33
Female age	0.23	0.08	8.92**	0.09	0.09	0.93
ALR	0.20	0.04	31.96***	0.11	0.03	11.29***
Female age ²	-0.05	0.01	12.06***	-0.02	0.02	2.25
Female (r)	3.16	0.19		1.98	0.12	
Year (r)	0.52	0.15		0.49	0.14	
Area (r)	3.18	7.63		0.03	0.03	

Estimates for random effects are marked by (r). Shown are parameter estimates with standard errors and significance (** $P < 0.01$, *** $P < 0.001$).

ALR, age at last reproduction.

Bouwhuis *et al.*, 2009). Here, we extended these analyses of offspring number to test for trans-generational effects of maternal age on the quality of recruited offspring.

We found no evidence for an effect of maternal age on offspring reproductive lifespan. Hence, whereas survival over the first year of life (i.e. survival to recruit to the breeding population) is compromised in offspring hatched from older mothers (Bouwhuis *et al.*, 2009), survival during subsequent reproductive life is not. We therefore have no evidence for a classic Lansing effect (i.e. offspring longevity declining with maternal age, Lansing, 1947) in great tits, although this effect is commonly found in laboratory model species (Priest *et al.*, 2002), including vertebrates (Tarin *et al.*, 2005). Future studies may be able to test whether the absence of a Lansing effect is generally true in natural populations.

In contrast, our key result suggests that the effect of maternal age on offspring fitness becomes apparent through offspring reproduction and is mediated through differences in survival of the grand-offspring (to hatching, fledging, or recruitment) as a function of both maternal age and grand-maternal age when the mother was hatched. This follows from our finding that offspring hatched from older mothers are more successful in recruiting offspring early in life, but then suffer from advanced and stronger deterioration in reproductive performance later in life, despite laying the same number of eggs as offspring hatched from younger mothers. This finding resembles one in *Drosophila*, where daughters born from mothers which had mated more often, and were producing fewer offspring themselves, experienced enhanced early life, but reduced late-life, fertility (Priest *et al.*, 2008). What could be the mechanism underlying such alternative life-history trajectories, in our case linking age-effects across generations? One possibility is

that older mothers, whilst themselves suffering from physiological deterioration outweighing increased breeding experience, can still socially transfer their accumulated knowledge to their offspring (Maestripieri & Mateo, 2009). Increased early life reproductive output in these offspring might then be associated with higher costs of reproduction, exacerbating senescence later in life (as in Nussey *et al.*, 2007; Descamps *et al.*, 2008; Reed *et al.*, 2008). Besides transmission of skills, the likelihood of territory inheritance could be increased in offspring hatched from older mothers. However, low annual survival rates, as well as sex-biased dispersal by females in the great tit (e.g. Szulkin & Sheldon, 2008), which is independent of maternal age (Bouwhuis *et al.*, 2009), suggest that this effect is unlikely to account for the patterns observed in our population. Alternatively, and with a more physiological basis, offspring hatched from older mothers might optimize their reproductive effort in response to having a low residual reproductive value, for example because of expected costs of catch-up growth or increased costs of reproduction, which would drive them to invest more in early life reproduction, but suffer from accelerated senescence. Recent findings that fitness traits in offspring can be affected by genomic imprinting effects in response to changes in the maternal environment (e.g. Hager *et al.*, 2009; although we are unaware of an example in birds), provide a potential mechanism for this scenario, and might underlie such a maternal effect (Mousseau & Fox, 1998b; Wolf, 2000). A third possibility is that lower maternal reproductive value, resulting from lowered survival prospects in older mothers, selects for increased early life reproductive effort in their daughters owing to reduced likelihood of maternal-offspring competition. Again, however, low annual survival rates and female-biased dispersal suggest that this may be a relatively weak effect in the great tit, compared to the potential effects in primates (Cant & Johnstone, 2008). Why such processes would only affect offspring reproduction, and not survival, is also unclear, and a better understanding of offspring physiology and behaviour in relation to maternal age is clearly required to start answering this fascinating question.

Finally, our analyses show that there is no effect of maternal age on offspring lifetime reproductive success. This contrasts with recent findings of a quadratic effect of maternal age on offspring LRS in female European rabbits *Oryctolagus cuniculus* reaching maturity (Rodel *et al.*, 2009), but seems robust given our large sample size and the extremely small parameter estimates for the maternal age-effects. The absence of an effect of maternal age on offspring LRS has two important implications. The first is that, although daughters hatched from different-aged mothers follow different life-history trajectories, these trajectories can be viewed as alternative strategies with the same overall fitness payoff, at least in the environment in which these birds were studied. However, a change in adult mortality rate would result in a

change in the relative fitness of these alternatives. The second implication is that average post-recruitment offspring quality is similar for mothers of all ages, implying that senescence estimates based on numbers of recruited offspring (as in Bouwhuis *et al.*, 2009) are likely to be unbiased, at least in our study system. This last implication is also supported by our analysis of the effect of female age on her number of grand-recruits; whereas female age² is a good predictor of her number of grand-recruits, this relationship is no longer significant when controlling for the female's number of recruits produced.

In conclusion, this study has linked offspring age-specific reproduction to maternal age at conception and thereby identified a new factor underlying variation in rates of ageing in a natural population. Our data add to the small, but growing number of studies explaining variation in rates of ageing in the wild (Nussey *et al.*, 2007; Descamps *et al.*, 2008; Reed *et al.*, 2008) and suggest that such effects can, in addition to resulting from effects early in the life of focal individuals, be transmitted across generations. Further work will need, in addition to life-history differences, to focus on the possible physiological and epigenetic differences associated with age and its transmission across generations.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Parameter estimates with standard errors for the effect of maternal age (range 1–9) on daughter age-specific recruit production. Positive estimates show that daughters hatched from older mothers have better reproductive performance, whereas negative estimates indicate reproductive performance of daughters hatched from older mothers to be reduced.

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